Glomeris undulata Koch and *G. conspersa* Koch are conspecific. - Enzyme electrophoretic evidence and taxonomical consequences (Diplopoda: Glomeridae)

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Glomeris undulata Koch and G. conspersa Koch are conspecific. - Enzyme electrophoretic evidence and taxonomical consequences (Diplopoda: Glomeridae. - Syntopic and allotopic populations of *Glomeris undulata* and *G. conspersa* have been investigated with enzyme electrophoresis. There was no evidence for separate gene pools of these taxa. However, *G. romana*, a species supposed to be closely related to *G. undulata* and *G. conspersa*, prooved to be well differentiated based on allozyme data. We therefore conclude that the taxa *undulata* and *conspersa* are conspecific. Consequently, *G. conspersa* C. L. Koch, 1847, is a junior subjective synonym of *G. undulata* C. L. Koch, 1844 (nov. syn.). An analysis of the colour pattern provides arguments for the discussion why no intermediate forms exist.

Key-words: Diplopoda - *Glomeris* - revision - local alleles - morphology - distribution - new synonymy.

INTRODUCTION

Glomeris undulata C.L.Koch, 1844, and *G. conspersa* C.L.Koch, 1847, are traditionally treated as two closely related but distinct species (cf. VERHOEFF 1911). They may be separated with reliability only by the form of the dorsal dark spots on the segments 2 to 12. These spots are parallel-sided in *G. undulata* and convergent posteriorly in *G. conspersa* (seen in walking position). Transitional forms that could indicate interbreeding of these taxa are very rare and have been named *G. undulata* var. *pseudoconspersa* (but see also VERHOEFF (1928b) for a case of assumed hybridisation). *G. undulata* and *G. conspersa* are often found syntopic, and large parts of their ranges overlap. Within the scope of an analysis of the genetic differentiation of the Central European *Glomeris* species by means of enzyme electrophoretic methods, we also examined syntopic and allotopic populations of *G. undulata* and *G. conspersa*. For comparison we included *G. romana* Verhoeff, 1900, a species which is supposed to be closely related to *G. undulata* and *G. conspersa* (cf. VERHOEFF 1911) but with a mainly allopatric distribution.

MATERIAL AND METHODS

Population samples of *Glomeris undulata*, *G. conspersa*, and *G. romana* were analyzed genetically by using routine enzyme electrophoretic methods of our laboratory (SCHOLL *et al.* 1978). Vertical starch gel electrophoresis was conducted using the same buffer systems as in previous studies on *Glomeris* (HOESS *et al.* 1997). 18 enzyme loci were analyzed. The enzymes investigated and the loci scored (in brackets) are: aspartate aminotransferase (Aat-1, Aat-2), glyceraldehyd-3-phosphate dehydrogenase (Gapdh), glucose-6-phosphate isomerase (Gpi), hexokinase (Hk), leucine aminopeptidase (Lap), L-lactate dehydrogenase (Ldh-1, Ldh-2), malate dehydrogenase (Mdh-1, Mdh-2), malic enzyme (Me), mannose-6-phosphate isomerase (Mpi), peptidase (Pep), 6-phosphogluconate dehydrogenase (Pgd6), phosphoglucomutase (Pgm), superoxide dismutase (Sod-1, Sod-2) and sorbitol dehydrogenase (Sodh).

The zymograms were photographed on Polaroid for reference. We refer to observed electromorphs as alleles which are identified by their electrophoretic mobility (in mm) relative to electromorphs of previously studied species (HOESS *et al.* 1997). Mendelian inheritance of the alleles at a given locus was not tested by crossbreeding experiments but was concluded by analogy to results of previous studies of our laboratory (e.g. ZIMMERMANN & SCHOLL 1993). Allele frequencies and genetic distances were calculated with the BIOSYS-1 programme package (SWOFFORD & SELANDER 1989). Nei-distance D (NEI 1978) was used for the construction of an UPGMA dendrogram (SNEATH & SOKAL 1973). Bootstrap analysis was conducted with the PHYLIP programme package (FELSENSTEIN 1986-95). The bootstrap values are estimates from 100 replicates (bootstrap values levelled out at 100 replicates) with UPGMA as cluster algorithm and an unrooted consensus tree.

The following population samples (Fig. 1) were examined (number of specimens in brackets): *Glomeris undulata*: Switzerland: Bösingen (13), Brunnen (9), Ingenbohler Berg (15), Loucherhorn (6), Malans (6), Meride (7), Merishausen (8), Niderhorn (6), St-Gingolph (15); Germany: Ehingen (17); *G. conspersa*: Switzerland: Biel (10), Bösingen (20), Castagnola (3), Châtollion (14), Densbüren (10), Ingenbohler Berg (11), Loucherhorn (8), Malans (12), Meride (8), Merishausen (13), St-Gingolph (11), Valangin (10); Germany: Ehingen (20); France: Cruseilles (13); *G. romana*: Italy: Camaiore (18). Lucca (4).

Several other population samples have been collected (often with low sample sizes) and have been used in addition to literature data to produce a distribution map of the taxa *undulata* and *conspersa*.

Tergites of two selected specimens of *G. undulata* were drawn using a camera lucida. The specimens were turned around their axes in order to draw every part of the tergite in vertical view.

RESULTS

Allele frequencies of the 18 loci of all samples are given in Table 1. For unknown reasons, several specimens in most samples failed to show activity at some
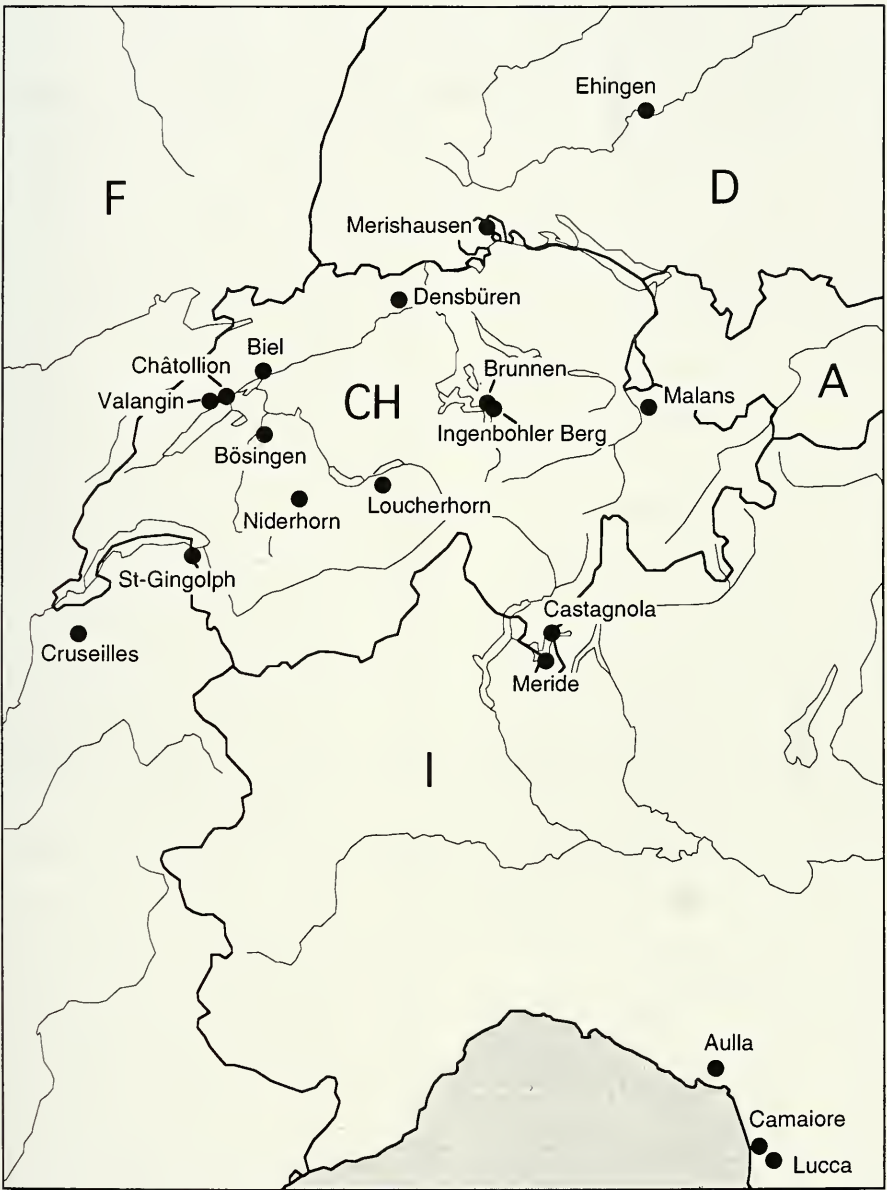
FIG. 1

Collecting sites in Switzerland and adjacent countries.

TABLE 1. - Allele frequencies at the 18 enzyme loci studied in *Glomeris undulata*, *G. conspersa* and *G. romana*. N = number of specimens scored at the respective locus.

Locus	Allele	G. undulata										G. conspersa														G. romana	
		Ehingen	Merishausen	Bösingen	St-Gingolph	Brunnen	Ingenbohler Berg	Loucherhorn	Niderhorn	Malans	Meride	Ehingen	Merishausen	Densbüren	Biel	Châtillon	Valangin	Cruseilles	Bösingen	St-Gingolph	Ingenbohler Berg	Loucherhorn	Malans	Castagnola	Meride	Lucca	Camaiore
Aat-1	111	-	0.25	-	-	-	-	-	-	-	-	-	-	-	-	0.04	-	-	-	-	-	-	-	-	-	-	-
	110	0.12	-	0.27	-	0.06	0.10	-	0.08	-	-	0.07	-	-	-	-	-	0.08	0.13	0.18	0.11	-	-	-	0.12	-	-
	108	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.12	0.06
	107	0.03	0.06	0.09	0.20	0.06	0.07	-	-	0.08	-	0.20	0.04	0.50	0.12	0.29	0.05	0.15	0.16	0.09	0.08	0.06	-	0.17	0.12	-	-
	105	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.08	-	-	-	-
	103	0.50	0.06	0.55	0.57	0.11	0.20	-	0.92	0.17	0.21	0.33	0.08	0.10	0.31	0.39	0.15	0.46	0.34	0.73	0.20	-	0.04	0.66	0.12	-	-
	102	-	0.25	-	-	0.33	0.16	0.92	-	-	0.07	-	0.42	-	-	-	0.25	0.08	0.03	-	0.22	0.75	-	-	-	-	-
	100	0.03	0.06	-	0.23	0.06	0.07	-	-	0.08	-	0.10	0.04	0.30	0.19	0.14	-	0.04	0.03	-	0.08	-	0.08	-	0.07	0.88	0.86
	97	-	-	-	-	0.06	-	-	-	-	0.72	-	-	-	-	-	0.05	-	-	-	-	0.13	-	0.17	0.57	-	-
	95	0.29	0.32	0.09	-	0.33	0.40	0.08	-	0.67	-	0.30	0.42	0.10	0.38	0.14	0.45	0.19	0.31	-	0.31	0.06	0.8	-	-	-	-
	93	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.05	-	-	-	-	-	-	-	-	-	0.08
	(N)	17	8	11	15	9	15	6	6	6	7	20	12	10	8	14	10	13	19	11	18	8	12	3	8	4	18

Aat-2

Allele																										
102	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
100	1	0.94	1	0.89	1	1	1	1	1	1	1	0.81	1	1	1	1	1	1	1	1	1	1	1	1	1	1
96	-	0.06	-	0.11	-	-	-	-	-	-	-	0.19	-	-	-	-	-	-	-	-	-	-	-	-	-	-
(N)	17	8	13	15	9	15	6	6	6	7	20	13	10	10	14	10	13	20	11	18	8	12	3	8	4	18

Gapdh

Allele																										
111	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.06	-	-	-	-	-	-	-	-	-	-	-
109	0.40	0.31	0.44	0.43	0.72	0.57	0.50	0.17	0.25	1	0.29	0.50	0.65	0.44	0.45	0.10	0.50	0.15	0.30	0.38	0.17	0.37	1	0.79	-	0.06
103	-	-	0.12	-	-	-	-	-	-	-	-	-	-	-	-	-	0.11	0.08	0.10	-	0.08	-	-	-	-	-
100	0.60	0.69	0.44	0.57	0.28	0.43	0.50	0.83	0.75	-	0.71	0.50	0.35	0.50	0.55	0.90	0.39	0.77	0.60	0.62	0.67	0.63	-	0.21	1	-
98	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0.94
97	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.08	-	-	0.08	-	-	-	-	-
(N)	15	8	8	14	9	15	5	6	6	7	19	11	10	10	9	11	13	13	10	17	6	12	2	7	4	16

Gpi

Allele																									
100	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
(N)	17	8	13	15	9	15	5	6	6	7	20	12	10	14	13	20	11	19	7	12	3	8	4	18

Hk

Allele		
114	-	-
112	-	0.04
	0.05	-

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107	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.11	–	–	–	–	–	–	–	–	–
103	0.50	0.63	0.65	0.37	0.17	0.27	0.08	0.08	0.07	0.45	0.19	0.70	0.35	0.50	0.25	0.62	0.32	0.32	0.25	0.06	0.12	0.67	0.19	0.25	0.06
100	0.50	0.37	0.31	0.63	0.83	0.73	0.92	0.92	0.93	0.55	0.81	0.30	0.65	0.50	0.75	0.27	0.68	0.68	0.75	0.94	0.88	0.33	0.81	0.75	0.94
(N)	17	8	13	15	9	15	6	6	7	20	13	10	10	14	10	13	17	10	19	8	12	3	8	4	18

Lap																			
118	–	–	–	–	–	–	–	–	–	0.12	–	–	–	–	–	–	–	–	–
109	–	–	–	–	–	–	–	–	0.37	0.50	–	–	–	–	–	–	–	–	–
104	–	0.18	–	–	–	–	–	–	–	–	–	0.06	–	–	–	–	–	–	–
102	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
100	1	0.73	1	1	0.86	0.66	0.25	1	0.63	0.38	1	0.75	0.78	–	0.88	1	0.80	0.86	0.91
99	–	0.09	–	–	–	0.17	–	–	–	–	1	0.19	0.22	0.75	0.12	–	0.20	0.14	0.09
97	–	–	–	–	–	–	–	–	–	–	–	–	–	0.25	–	–	–	–	–
(N)	9	11	1	3	7	6	6	1	8	8	1	8	8	4	8	8	7	6	5	11

Ldh-1																
105	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.06	–	–	–	–	–
103	–	0.06	0.03	–	–	0.08	–	0.25	0.03	0.29	0.25	0.54	0.39	0.10	0.29	0.31	0.03	0.33	0.50	0.25
100	0.63	0.31	0.56	0.43	0.61	0.47	0.67	0.50	0.58	0.79	0.64	0.29	0.28	0.44	0.08	0.17	0.40	0.34	0.47	0.13	0.56	0.31	0.44	0.46	0.33	0.44	0.22
96	0.37	0.63	0.38	0.54	0.39	0.50	0.17	0.33	0.17	0.21	0.33	0.42	0.44	0.31	0.38	0.44	0.50	0.34	0.50	0.19	0.21	0.17	0.31	0.78	–

(continued)

	12	8	8	14	9	15	6	6	7	18	12	9	8	12	9	8	16	8	19	8	12	3	8	4	18
94	-	-	-	-	0.03	-	-	-	-	-	-	-	-	-	0.03	0.08	0.17	-	-	-	-	-	-	-	-
(N)	12	8	8	14	9	15	6	6	7	18	12	9	8	12	9	8	16	8	19	8	12	3	8	4	18

Ldh-2

	14	7	12	14	9	14	6	4	4	18	7	5	5	3	9	8	16	8	16	7	11	3	6	4	13
105	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
103	-	-	-	-	-	0.07	0.08	-	-	-	0.07	-	-	-	0.06	-	-	-	0.06	-	-	-	-	-	-
100	0.89	1	0.17	0.93	0.72	0.50	0.75	0.25	0.75	0.78	0.72	1	1	1	0.72	1	0.28	1	0.56	0.64	0.45	0.83	0.42	-	-
96	0.07	-	-	-	-	-	-	-	-	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
94	0.04	-	0.83	0.07	0.28	0.43	0.17	0.50	0.25	0.19	0.21	-	-	-	0.22	-	0.72	-	0.38	0.36	0.41	0.17	0.58	-	-
80	-	-	-	-	-	-	-	0.25	-	-	-	-	-	-	-	-	-	-	-	-	0.14	-	-	-	0.11
72	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0.89
(N)	14	7	12	14	9	14	6	4	4	18	7	5	5	3	9	8	16	8	16	7	11	3	6	4	13

Mdh-1

	14	7	12	14	9	14	6	4	4	18	7	5	5	3	9	8	16	8	16	7	11	3	6	4	13
112	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.06	-	-
110	-	-	-	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	0.25	-
107	-	-	-	-	-	-	-	-	-	-	0.04	-	-	-	-	-	-	-	-	-	-	-	0.68	0.75	-
102	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.23	-	-
100	1	1	1	0.97	1	1	1	0.90	1	1	0.96	1	1	1	0.93	1	1	1	0.88	0.94	1	0.83	-	-	-
94	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.07	-	-	-	0.12	0.06	-	0.17	-	-	-

Mdh-2

	(N)	100	99	98	97	96	95	93	91	88
	14	0.86	-	-	0.11	-	-	-	0.03	-
	8	0.81	-	0.19	-	-	-	-	-	-
	10	0.60	0.15	-	0.10	0.10	0.05	-	-	-
	15	1	-	-	0.07	-	-	-	-	-
	9	0.94	-	0.06	-	-	-	-	-	-
	6	0.90	-	-	-	-	0.08	-	-	-
	6	0.92	-	0.08	-	0.08	-	-	-	-
	6	0.92	-	0.08	-	-	-	-	-	-
	7	0.92	-	-	-	-	-	-	-	-
	18	0.94	-	0.06	-	-	-	-	-	-
	13	1	-	-	-	-	-	-	-	-
	10	0.90	-	-	-	-	-	-	0.10	-
	9	0.83	-	0.17	-	-	-	-	-	-
	12	0.94	-	-	0.06	-	-	-	-	-
	10	0.50	0.17	-	0.25	0.03	0.06	-	-	-
	18	0.86	0.03	-	0.03	-	-	0.05	0.03	-
	19	0.90	0.05	-	-	-	-	-	0.05	-
	8	1	-	-	-	-	-	-	-	-
	12	0.94	0.17	-	-	-	0.04	-	-	-
	10	0.96	-	0.06	-	-	-	-	-	-
	18	0.32	-	-	-	-	0.17	-	0.10	-
	8	0.94	-	0.06	-	-	-	-	-	-
	3	0.94	0.17	0.17	-	-	-	-	0.17	-
	8	-	-	0.06	-	-	-	-	-	-
	4	1	-	-	-	-	-	-	-	-
	18	1	-	-	-	-	-	-	-	-

Me

	(N)	108	106	102	100
	14	-	-	0.13	0.77
	8	-	-	0.20	-
	10	-	0.31	0.23	0.50
	15	-	-	0.22	0.77
	9	-	-	0.25	0.11
	6	-	-	0.20	0.07
	6	-	-	0.08	0.20
	6	-	-	0.20	0.60
	7	-	-	0.17	0.33
	18	-	-	0.10	0.66
	13	-	-	0.15	-
	10	-	-	0.33	0.56
	9	-	-	0.22	0.61
	12	-	-	0.58	-
	10	-	-	0.50	0.19
	18	-	-	0.14	0.86
	19	-	-	0.09	0.75
	8	-	-	0.05	0.95
	12	-	-	0.37	0.16
	10	-	-	0.05	0.69
	18	-	-	0.95	0.29
	8	-	-	0.21	0.29
	3	-	-	0.42	0.33
	8	0.03	-	0.33	-
	4	-	-	1	-
	18	0.03	-	0.97	-

98	0.23	0.50	0.30	-	0.67	0.64	0.60	0.92	0.10	0.33	0.24	0.81	0.11	0.17	0.42	-	-	-	0.16	-	0.47	0.50	0.31	1	0.17	-
96	-	0.31	-	-	-	-	-	-	0.10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
94	-	0.06	-	-	0.04	-	-	-	-	-	-	0.04	-	-	-	-	-	-	-	-	-	-	-	-	-	-
92	-	-	-	-	-	-	-	-	-	0.17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.08	-
(N)	13	8	5	13	9	14	5	6	6	6	19	13	9	9	12	8	7	16	10	19	7	8	1	6	4	18

Mpi

104	-	-	-	-	0.03	0.08	-	0.08	0.07	-	-	-	-	-	-	-	-	-	0.05	0.13	-	0.17	-	-	-	-
100	0.94	0.56	0.65	0.90	0.83	0.90	1	0.92	0.72	0.95	0.77	0.40	0.78	0.68	0.60	0.85	0.60	0.86	0.87	0.81	0.83	0.83	0.75	0.11	1	0.78
97	0.06	0.44	0.35	0.10	0.17	0.07	-	-	0.14	0.05	0.23	0.60	0.22	0.32	0.40	0.15	0.40	0.14	0.08	0.06	0.17	-	0.25	-	-	0.11
91	-	-	-	-	-	0.08	-	-	0.07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
(N)	17	8	13	15	9	15	6	6	7	20	13	10	9	14	10	13	20	11	19	8	12	3	8	4	18	—

Pep

102	-	0.13	0.31	-	-	0.10	0.25	-	0.20	-	-	-	-	-	-	1	0.06	-	0.03	0.28	-	-	-	-	-	0.15
100	0.47	0.81	0.69	0.75	1	0.64	0.42	0.92	0.80	1	0.58	0.67	1	0.95	0.86	0.80	-	0.86	0.67	0.87	0.36	0.75	0.83	0.94	1	0.82
98	0.09	0.06	-	-	-	0.23	-	0.08	-	-	0.03	0.33	-	-	0.14	0.20	-	0.08	-	0.10	-	0.05	0.17	0.06	-	0.03
96	0.44	-	0.25	-	-	0.03	0.33	-	-	-	0.39	-	-	0.05	-	-	-	-	0.33	-	0.36	0.20	-	-	-	-
(N)	17	8	13	14	9	15	6	6	5	7	19	12	10	10	14	10	11	18	9	19	7	10	3	8	4	17

Pgd6

Pop. (N)	108	104	100	96	94
13	-	-	1	-	-
7	-	-	1	-	-
6	-	-	0.92	0.08	-
13	-	-	1	-	-
9	-	-	1	-	-
15	-	-	1	-	-
6	-	-	1	-	-
5	-	-	1	-	-
5	-	-	1	-	-
6	-	-	1	-	-
17	-	-	1	-	-
12	-	-	1	-	-
7	-	-	0.93	0.07	-
10	-	-	1	-	-
10	-	-	1	-	-
8	-	-	0.94	0.06	-
4	-	-	1	-	-
13	-	-	1	-	-
10	-	-	1	-	-
19	-	-	1	-	-
8	-	-	1	-	-
11	-	-	1	-	-
3	-	-	1	-	-
8	-	-	1	-	-
4	-	-	0.88	-	0.12
17	-	-	0.97	0.03	-

Pgm

Pop. (N)	103	100	97	96	94	93	91	89	85	81	77
13	0.14	0.68	-	-	0.18	-	-	-	-	-	-
7	0.11	0.58	0.14	-	0.14	-	-	-	-	-	-
6	0.10	0.11	0.33	-	0.45	-	-	-	-	-	-
13	-	0.63	0.07	-	0.20	-	0.06	-	-	-	-
9	-	0.94	-	-	-	-	0.06	-	-	-	-
15	0.10	0.80	-	-	0.03	-	0.07	-	-	-	-
6	0.17	0.83	-	-	-	-	-	-	-	-	-
5	-	0.50	0.50	-	-	-	-	-	-	-	-
5	0.33	0.59	-	-	-	-	-	-	-	0.08	-
6	0.07	0.79	-	-	-	-	-	-	-	0.07	0.07
17	0.19	0.75	-	-	0.06	-	-	-	-	-	-
12	0.22	0.68	-	-	0.10	-	-	-	-	-	-
7	0.05	0.60	0.30	-	0.05	-	-	-	-	-	-
10	0.11	0.61	-	-	0.17	-	-	0.11	-	-	-
10	0.10	0.79	-	-	0.11	-	-	-	-	-	-
8	-	0.72	0.22	-	0.06	-	-	-	-	-	-
4	-	0.40	0.40	-	0.15	0.05	-	-	-	-	-
13	0.40	0.34	0.15	-	0.11	-	-	-	-	-	-
10	0.17	0.72	-	0.11	-	-	-	-	-	-	-
19	0.11	0.84	-	0.05	-	-	-	-	-	-	-
8	0.25	0.69	-	-	-	-	-	0.06	-	-	-
11	0.05	0.95	-	-	-	-	-	-	-	-	-
3	0.17	0.83	-	-	-	-	-	-	-	-	-
8	-	0.94	0.06	-	-	-	-	-	-	-	-
4	-	-	-	0.63	-	0.37	-	-	-	-	-
17	-	0.06	-	0.60	-	0.34	-	-	-	-	-

(N)	14	7	9	15	9	6	6	6	7	16	11	10	9	12	9	10	16	9	19	8	10	3	8	4	16
Sod-1																									
115	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
113	-	-	0.11	-	-	0.04	0.08	0.08	0.17	0.29	-	-	-	0.04	-	-	0.05	0.05	0.21	0.06	0.08	-	-	-	-
111	0.15	-	0.28	0.29	0.50	0.25	0.08	0.08	-	0.29	0.17	0.25	0.10	0.11	0.17	0.08	0.05	0.09	0.11	0.19	0.04	1	0.63	-	-
100	0.85	1	0.61	0.71	0.50	0.71	0.84	0.84	0.83	0.42	0.83	0.75	0.90	0.85	0.83	0.92	0.90	0.86	0.68	0.75	0.88	-	0.31	-	-
(N)	17	7	9	14	9	6	6	6	7	20	13	10	10	13	9	12	19	11	19	8	12	3	8	4	18

(N)	17	8	13	9	15	5	5	6	6	16	13	10	7	7	7	13	18	8	16	7	10	3	8	4	16
Sod-2																									
100	-	0.25	0.15	0.35	-	0.10	0.10	0.40	0.17	0.75	0.06	0.27	0.10	-	-	-	0.27	0.08	0.13	0.13	0.36	0.10	0.67	0.19	-
98	0.24	0.13	-	0.23	0.39	-	-	-	-	-	0.25	0.08	0.50	0.57	0.50	0.43	0.11	0.18	0.06	-	0.20	-	0.19	-	0.06
95	0.29	0.43	0.85	0.19	-	0.30	0.10	0.60	-	0.17	0.06	0.27	0.30	0.43	0.07	0.14	0.53	0.43	0.34	0.14	-	-	0.19	0.88	0.53
93	-	0.06	-	-	0.33	0.23	0.40	-	0.17	0.08	0.25	0.38	-	-	0.29	-	-	0.28	0.13	0.41	0.29	0.45	0.33	0.25	-
91	0.47	-	-	0.23	0.28	0.20	0.40	0.66	-	-	0.38	-	0.10	-	0.14	0.43	-	0.13	0.06	0.21	0.25	-	0.19	-	0.13
88	-	0.13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.12	0.25
79	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03
(N)	17	8	13	9	15	5	5	6	6	16	13	10	7	7	7	13	18	8	16	7	10	3	8	4	16

(N)						0.33												0.13	0.21						0.06
Sodh																									
114	-	-	-	-	0.17	0.33	-	-	-	-	-	-	-	-	-	-	-	0.13	0.21	-	-	-	-	-	0.06

Allele																										
110	-	-	-	-	0.08	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
108	0.72	0.75	-	-	0.13	0.13	-	0.05	-	-	-	-	-	-	-	-	-	-	-	-	-	0.07	-	0.04	-	-
106	-	-	-	-	-	0.13	0.03	-	-	-	-	-	-	-	0.04	0.03	-	-	-	0.17	-	-	-	-	-	0.03
103	0.06	0.13	-	-	0.13	0.06	-	-	-	-	-	-	-	-	-	-	-	0.17	-	-	-	0.06	0.07	-	0.03	-
100	0.16	0.13	0.94	0.83	0.45	0.68	0.97	0.95	1	1	1	0.89	1	1	0.96	0.97	0.86	0.50	1	0.66	1	0.94	0.93	0.96	1	0.97
96	-	-	-	-	-	-	-	-	-	-	-	0.11	-	-	-	-	-	-	-	0.17	-	-	-	-	-	-
92	-	-	-	0.17	-	-	-	-	-	-	-	-	-	-	-	-	0.07	-	-	-	-	-	-	-	-	-
86	-	-	0.06	-	-	-	-	-	-	-	-	-	-	-	-	-	0.07	-	-	-	-	-	-	-	-	-
(N)	18	4	8	3	12	8	19	10	19	10	10	14	8	10	13	17	7	6	6	6	14	9	15	13	8	15

loci or their zymograms were not scorable. These specimens were not included for calculations of allele frequencies at the respective loci. Therefore, the number of specimens is not always identical in Table 1 for all loci scored in a particular population. Most enzyme loci are highly polymorphic in all three taxa, viz. *Glomeris undulata*, *G. conspersa* and *G. romana*.

Although the samples of *G. undulata* and *G. conspersa* cover large parts of the ranges of these taxa, only minor variation in allele frequencies of the respective populations was observed. While *G. romana* differs from *G. undulata* and *G. conspersa* at several loci by allele substitution (Sod-1) or highly different allele frequencies (Aat-1, Gapdh, Ldh-2, Mdh-1, Mpi, Pgm, Sodh), *G. undulata* and *G. conspersa*, in contrast, usually show the same alleles and very similar frequencies. The analysis of the distribution of rare alleles reveals that some local alleles which were each found at one locality only, are present in both *G. undulata* and *G. conspersa* from the particular locality. These local alleles are: Aat-2^{96} in the Merishausen sample, allele Me^{92} at Meride, allele Ldh-2^{96} at Ehingen, allele Ldh-2^{80} at Malans and allele Sodh^{86} at Meride.

The UPGMA dendrogram that resulted from a cluster analysis of the populations according to their genetic distances is shown in Fig. 2. *G. romana* is clearly separated from the other two taxa with an average genetic distance (Nei-D) of 0.65 and a bootstrap value of 100. *G. undulata* and *G. conspersa*, in contrast, do not form separate clusters. The syntopic samples are of particular interest because in seven from eight such situations studied, *G. undulata* and *G. conspersa* from the same locality cluster with lowest genetic distances, and four of these clusters are supported by bootstrap values > 70 (Fig. 2). Genetic distances among the *undulata/conspersa* populations are rather low. Thus, separations of the samples according to geographical regions or differentiations according to geographical distances are not evident.

DISCUSSION

Several species of the genus *Glomeris* are known to be highly variable in their colour pattern, and about 400 varieties, including the nominotypic varieties, have been described which belong to about 70 nominal species (many names, however, are not available according ICZN Art. 16 + 45f, g). If the biological species concept (e.g. MAYR & ASHLOCK 1991) is applied that defines species as genetic units of naturally interbreeding populations which are reproductively isolated from other such groups, allozyme data provide a very powerful tool to test whether or not two taxa or forms share a common gene pool and thus belong to the same species. Species boundaries and specific separation within the genus *Glomeris* have recently been successfully analysed with allozyme data (HOESS *et al.* 1997) where *G. intermedia* Latzel, 1884, was shown to be a separate species, contrary to traditional taxonomy that treated *G. intermedia* as a subspecies of *G. hexasticha* Brandt, 1833.

G. undulata and *G. conspersa* have always been treated as two distinct species which are assumed to be closely related. Intermediate forms that might indicate hybrids have not been observed even though both taxa are often found syntopic and
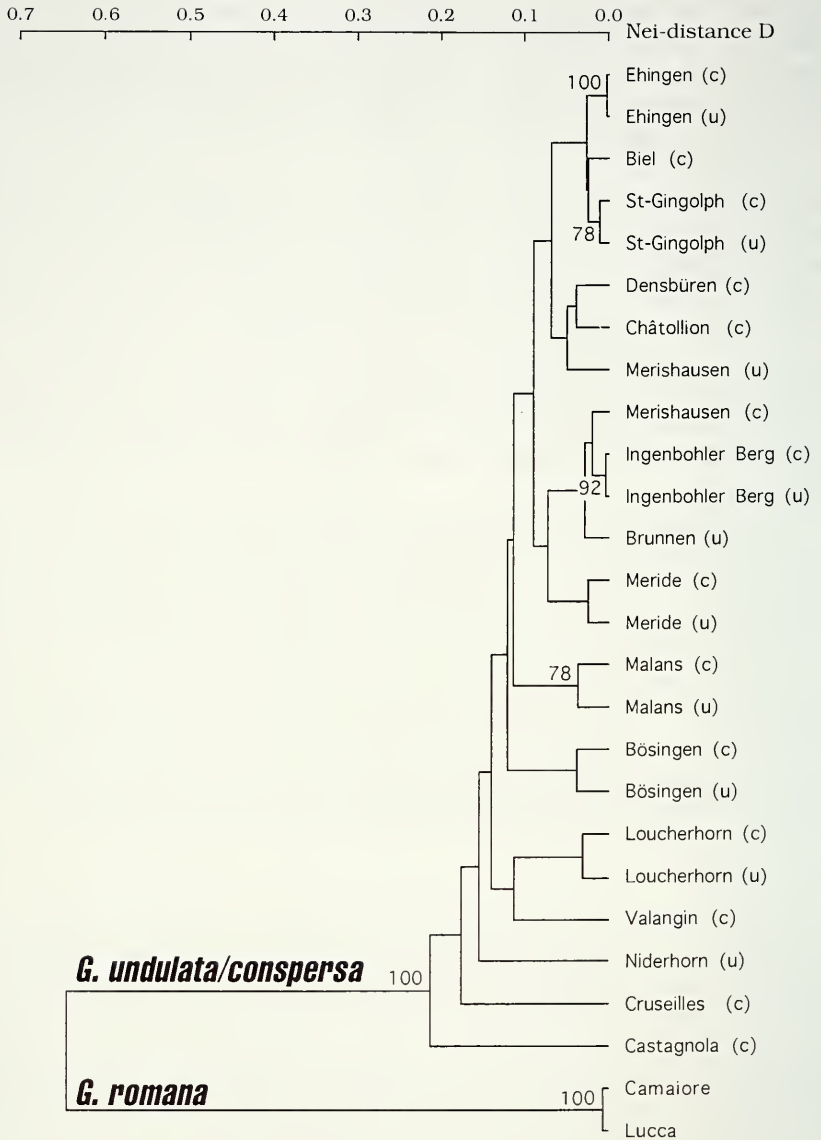
FIG. 2

UPGMA dendrogram based on Nei-distance D values in pairwise comparisons of populations of *Glomeris undulata* (u), *G. conspersa* (c) and *G. romana*. Bootstrap values > 70 are indicated (percentage over 100 replicates).

large parts of their ranges overlap. Only VERHOEFF (1901) described a light form of *G. undulata* as var. *pseudoconspersa* indicating to him a mixture of the colour pattern of both taxa, and, later, postulated some hybrids (VERHOEFF 1928b, p. 320-321). Thus, as judged from the colour patterns, specific separation of *G. undulata* and *G. conspersa* seems to be completed despite some rare possible hybrids. The genetic basis of variation in colour patterns, however, has never been analysed in *Glomeris*. The difference in the colour patterns of *G. undulata* and *G. conspersa* might result from two alleles in a dominant/recessive relation at a single locus. In this case, we would not expect to find intermediate forms.

ALLOZYME DATA

Based on the allozyme data, there is no evidence for separate gene pools of *G. undulata* and *G. conspersa*. The alleles observed and their frequencies are rather similar in all populations of both taxa. Consequently, the degree of genetic differentiation of all populations studied is very low. Furthermore, the analysis of the distribution of rare alleles is very informative because it revealed that local alleles (cf. BUSACK 1986) are repeatedly found in syntopic populations of both taxa. The Aat-2 locus is of particular interest because this locus is highly conservative in *Glomeris* (HOESS *et al.* unpublished), most *Glomeris* species are fixed for the allele Aat-2^{100}, and allele Aat-2^{96} is only found at the locality Merishausen where it was recorded in both *G. undulata* and *G. conspersa*.

In the dendrogram, the populations of *G. undulata* and *G. conspersa* do not form separate clusters, but syntopic populations of both taxa usually cluster at lowest levels of genetic differentiation, and most of these clusters are supported by bootstrap values > 70. Consequently, we regard the taxa *G. undulata* and *G. conspersa* as a single species (see "Conclusion" below) and treat conspersa in the following as a form of *G. undulata*. In comparison to *G. undulata/conspersa*, *G. romana* clearly has a separate gene pool. Genetic differentiation, however, is rather low. This agrees with current classification where *G. romana* is assumed to be closely related to *G. undulata/conspersa* (VERHOEFF 1911).

COLOUR PATTERN

Although both forms of *G. undulata* (nominate form and f. *conspersa*) are often found syntopically, no transition in colour pattern is known. In fact, *G. undulata* var. *pseudoconspersa* and the "hybrids" of VERHOEFF (1928b) do not represent transition forms at the dorsal spots, that means from the parallel spots of *undulata* to the convergent spots of *conspersa*. Instead, VERHOEFF (1928b) used the colour pattern of the remaining parts of the tergites to qualify these specimens as transitional. Consequently, the question remains: why are the two forms of *G. undulata* separated so strictly?

A specially patterned *G. undulata* specimen (from near Mendrisio in Ticino, Switzerland) may help to understand the real nature of the colour pattern of *G. undulata*. The fifth tergite of this specimen is illustrated in Fig. 3a. Unlike most individuals of this species where the speckles seem to be scattered irregularly next to the central spot, the speckles of this specimen are arranged in a sinuous line that strikingly
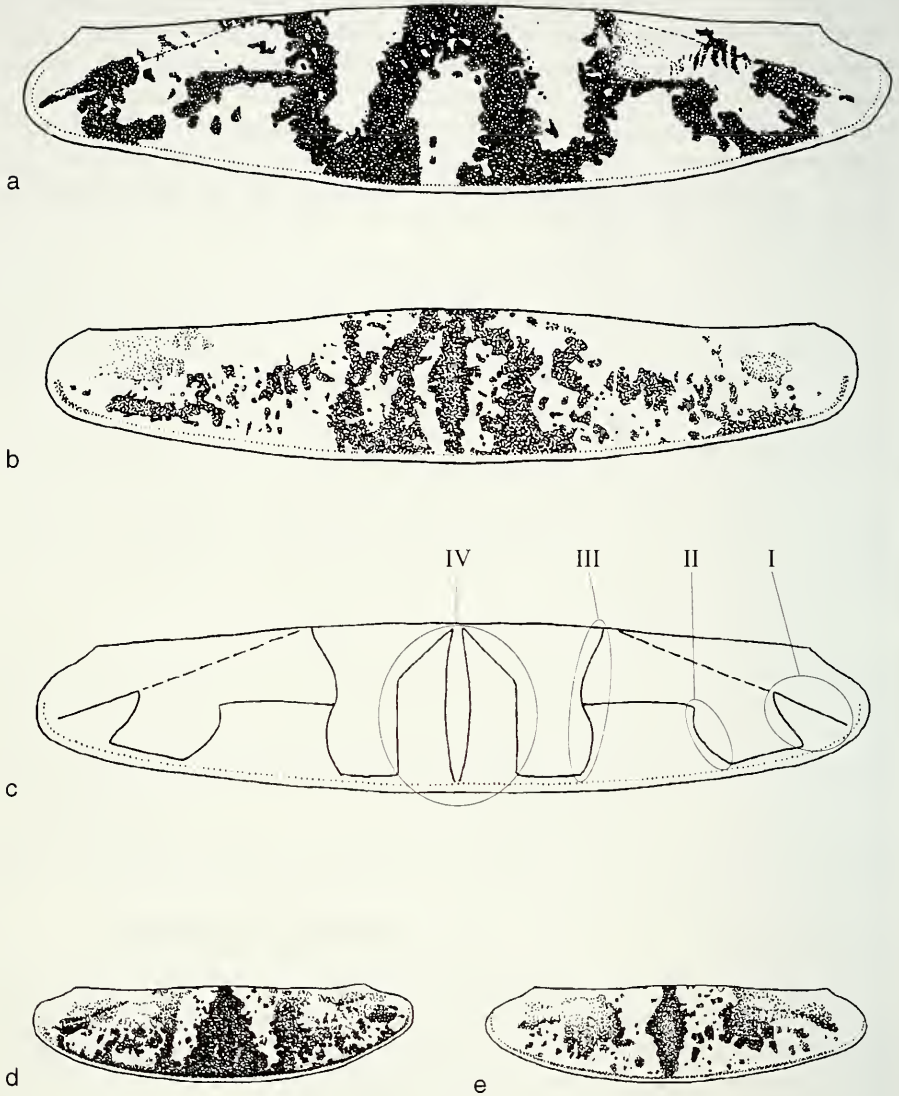
FIG. 3

Vertical view of the fifth tergite of *Glomeris undulata*: a) a specimen from Mendrisio (Switzerland), b) a specimen from Ingenbohler Berg (Switzerland), c) schematic diagram of the basic pattern of *G. undulata* (sinuous line) with the nomenclature of the dark spots sensu VERHOEFF (1928a), d) "normally coloured" specimen of nominate form, e) "normally coloured" specimen of f. *conspersa*.

resembles the dark spots of many other *Glomeris* species. Possibly, this specimen reflects the original pattern of *G. undulata*. Varieties with a light spot IV (sensu VERHOEFF 1928a) between the dark spots IV (as in the illustrated specimen) are already known. But this pattern cannot explain the difference in the central dark spot between the nominate form and f. *conspersa*. However, other varieties are known - e.g. the specimen shown in Fig. 3b (from Ingenbohler Berg) - that show an additional dark spot in the light spot IV. From these two specimens we can conclude a basic pattern for the species which is illustrated in Fig. 3c. The sinuous line (with an extra line in the region of the muscular insertions on the prozonite) may be traced from one side to the other. In real specimens, certain parts of this sinuous line may be invisible due to non-expression of the dark pigment or they may be connected by dark pigment filling up the space between the dark spots. Thus, we can conclude that in the nominate form of *G. undulata* the dark spots IV are well expressed and normally connected, and that in f. *conspersa* only the dark spot within the light spot IV - in Verhoeff's terminology this dark spot was treated as part of the dark spots IV - is well expressed and the normal dark spots IV are missing. With this argumentation no transition between the nominate form of *G. undulata* (Fig. 3d) and the form *conspersa* (Fig. 3e) can be imagined. A single gene or a group of coupled genes may be responsible for the expression or absence of the dark spots IV.

DISTRIBUTION

Fig. 4 shows the distribution of *G. undulata* (nominate form and f. *conspersa*) based on a compilation of literature data and on own collections. In large parts of its range, *G. undulata* is present only in one form. The reasons for this sitation are not known. But if the above hypothesis of the genetic basis of the two forms would be confirmed experimentally, the discordant distribution of both forms could be explained by local differences in allele frequencies, either due to selection or stochastic processes.

CONCLUSION

As we have shown, there is no evidence for separate gene pools in syntopic populations of *Glomeris undulata* and *G. conspersa*. Thus, we conclude that these taxa are conspecific. Therefore, we consider *G. conspersa* C.L.Koch, 1847, as a junior subjective synonym of *G. undulata* C.L.Koch, 1844 (**nov. syn.**). There is no need to preserve the better known name *G. conspersa* because *G. undulata* has been used many times in the literature (at least 37 entries for *G. undulata* and at least 69 entries for *G. conspersa*).
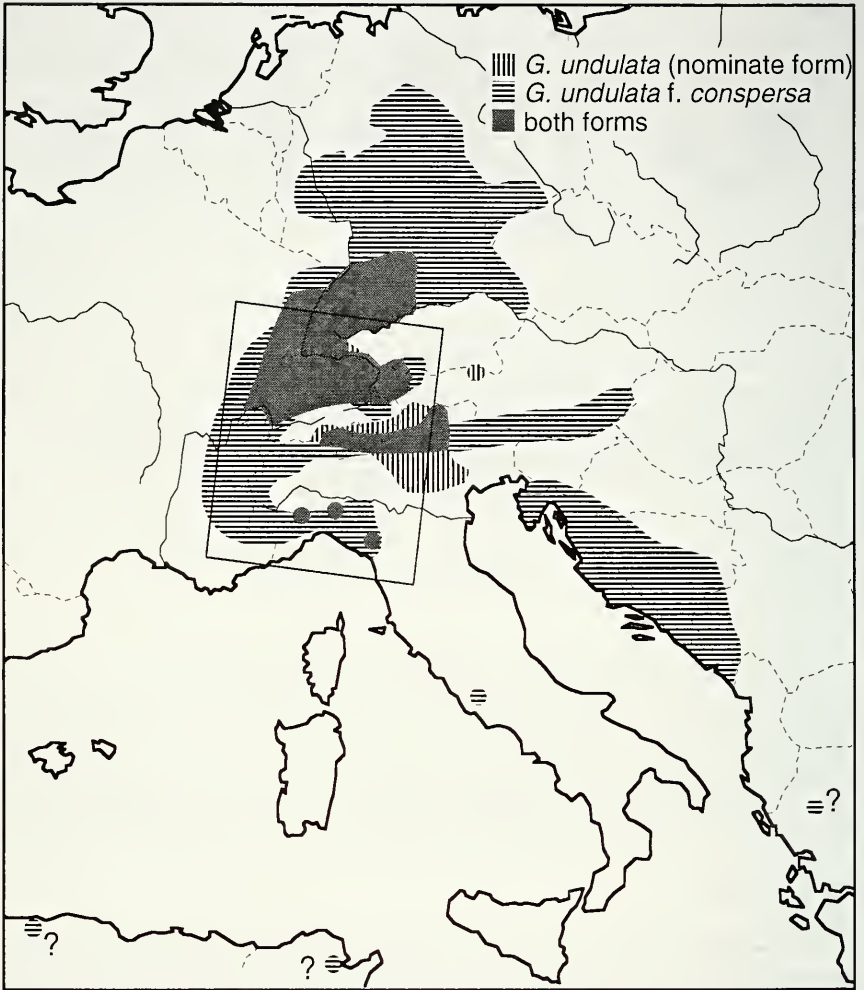
ACKNOWLEDGEMENTS

FIG. 4

Distribution of *Glomeris undulata* (nominate form and f. *conspersa*). The section covered in Fig. 1 is framed.

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